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Abstract: Facilitative effects of some species on others are a major driver of biodiversity. These positive effects of a benefactor on its beneficiary can result in negative feedback effects of the beneficiary on the benefactor and reduced fitness of the benefactor. However, in contrast to the wealth of studies on facilitative effects in different environments, we know little about whether the feedback effects show predictable patterns of context dependence. We reanalyzed a global data set on alpine cushion plants, previously used to assess their positive effects on biodiversity and the nature of the beneficiary feedback effects, to specifically assess the context dependence of how small- and large-scale drivers alter the feedback effects of cushion-associated (beneficiary) species on their cushion benefactors using structural equation modelling. The effect of beneficiaries on cushions became negative when beneficiary diversity increased and facilitation was more intense. Local-scale biotic and climatic conditions mediated these community-scale processes, having indirect effects on the feedback effect. High-productivity sites demonstrated weaker negative feedback effects of beneficiaries on the benefactor. Our results indicate a limited impact of the beneficiary feedback effects on benefactor cushions, but strong context dependence. This context dependence may help to explain the ecological and evolutionary persistence of this widespread facilitative system.

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The context-dependence of beneficiary feedback effects on benefactors in plant facilitation

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The manuscript contains 4 figures (Fig. 4 in color), 1 table and 5 appendices of supporting information.

Summary

- Facilitative effects of some species on others are a major driver of biodiversity. These positive effects of a benefactor on its beneficiary can result in negative feedback effects by the beneficiaries on the benefactor and reduced fitness of the benefactor. However, in contrast to the wealth of studies on facilitative effects in different environments we know little about whether the feedback effects show predictable patterns of context-dependence.
- We reanalyzed a global dataset on alpine cushion plants, previously used to assess their positive effects on biodiversity and the nature of the beneficiary feedback effects, to specifically assess the context-dependence of how small- and large-scale drivers alter the feedback effects of cushion-associated (beneficiary) species on their cushion benefactors using structural equation modelling.
- The effect of beneficiaries on cushions became negative when beneficiary diversity increased and facilitation was more intense. Local-scale biotic and climatic conditions mediated these community-scale processes, having indirect effects on the feedback effect. High-productivity sites demonstrated weaker negative feedback effects of beneficiaries on the benefactor.
- Our results indicate a limited impact of the beneficiary feedback effects on benefactor cushions, but strong context-dependence. This context-dependence may help to explain the ecological and evolutionary persistence of this widespread facilitative system.

Keywords: antagonistic plant-plant interactions, beneficiary feedback effect, competition, context-dependence, facilitation, nurse plant, parasitism, structural equation modelling

Introduction

Facilitation, i.e. the positive effects of one organism on others, is a common interaction among co-occurring plants (Callaway, 2007). Over the last two decades, important progress has been made in the understanding of the mechanisms of facilitation and its context dependence (Brooker *et al.*, 2008). Most facilitative effects consist of the amelioration of abiotically and biotically stressful conditions in ways that benefit other species (Stachowicz, 2001). Facilitative effects can consist of relief from physical stress (Callaway 1992; Bertness & Hacker, 1994; Bruno, 2000), resource supply that can be either direct (nutrients:

Turkington & Harper, 1979; water: Caldwell *et al.*, 1998) or indirect (nutrients: van der Heijden & Horten, 2009; water: Pugnaire *et al.*, 1996a), protection from herbivores (Smit & Ruifrok, 2011; Louthan *et al.*, 2014) or pollinator attraction (Reid & Lortie, 2012). All of these mechanisms of facilitation share the common result in which one species ameliorates the limiting environmental conditions of another species, thereby creating improved or even newly suitable environmental conditions at fine scales in an otherwise less suitable or unsuitable habitat (Bruno *et al.*, 2003; Schöb *et al.*, 2012; McIntire & Fajardo, 2013). Though facilitative processes occur at fine spatial scales, they can have important ecological consequences from local to global scales. Facilitative effects can increase species richness (Pugnaire *et al.*, 1996a; Michalet *et al.*, 2006; Cavieres *et al.*, 2014), conserve phylogenetic diversity (Valiente-Banuet *et al.*, 2006; Butterfield *et al.*, 2013), drive natural selection (Michalet *et al.*, 2011), and improve ecosystem services (Mulder *et al.*, 2001; Li *et al.*, 2007; Badano & Marquet, 2009).

We know a great deal about the mechanisms and context-dependence of facilitative effects of benefactors on beneficiaries (Callaway, 2007), but our understanding on how facilitated (beneficiary) species feed back to benefactors is limited. Recent studies have shown that the close co-occurrence of benefactor and beneficiary species can induce a feedback effect of the beneficiary on the benefactor (hereafter called the Beneficiary Feedback Effect, or "BFE"; Supporting Information Fig. S1). BFEs can be positive (Pugnaire *et al.*, 1996b), resulting in a mutualism, but generally the effect has been shown to be negative, i.e. resulting in an antagonistic interaction, e.g. facultative parasitism (McAuliffe, 1984, 1988; Valiente-Banuet *et al.*, 1991; Flores-Martínez *et al.*, 1994; Holzapfel & Mahall, 1999; Michalet *et al.*, 2011; Cranston *et al.*, 2012; Schöb *et al.*, 2014a; Schöb *et al.*, 2014b). However, compared to the better-known co-occurring negative effects of competitive interactions (Keddy, 2001), we are just beginning to understand the mechanisms underlying reciprocal feedbacks that are associated with positive effects. In particular, from studies in arid environments we know that direct feedback effects from beneficiaries to benefactors occur, and that they likely involve competition for resources (Valiente-Banuet *et al.*, 1991; Holzapfel & Mahall, 1999; Schöb *et al.*, 2014a). However, we do not know if these BFEs are context-dependent, such as competitive and facilitative interactions in general (Bertness & Callaway, 1994; He *et al.*, 2013) and if so, whether they are related to the facilitative effect of the benefactor on the beneficiary, whether these effects depend on the composition of the beneficiary community, or if they are modulated by changing environmental conditions.

115 Therefore, a quantitative analysis of the context-dependence of feedbacks between
116 benefactors and beneficiaries will contribute substantially to understanding how relationships
117 among these species evolve, are sustained over generations, or wane in intensity over time.

118 Recent reports indicate that the frequency, intensity and importance of facilitative
119 effects of benefactors on beneficiaries are context-dependent (He *et al.*, 2013; Le Bagousse-
120 Pinguet *et al.*, 2014). For instance, the interaction can change during ontogeny from
121 facilitative at early life history stages of the beneficiary species to competitive at later stages
122 (Miriti, 2006; Stuhlz *et al.*, 2007; Armas & Pugnaire, 2009; Soliveres *et al.*, 2010; le Roux *et*
123 *al.*, 2013). Facilitation can also vary among functional groups of species, with competitive
124 species benefiting more from stress amelioration than stress-tolerant species (Liancourt *et al.*,
125 2005; Maestre *et al.*, 2009; Forey *et al.*, 2010). Similarly, the facilitative effects may also
126 depend on the tolerance of the particular prevailing stress by the benefactor and the ability of
127 the benefactor to ameliorate this stress (Michalet *et al.*, 2014). For example for cushion plants
128 it has been shown that the cushion morphology can change along environmental gradients,
129 including changes in the traits involved in facilitation, with significant consequences on the
130 facilitation effect (Michalet *et al.*, 2011; Schöb *et al.*, 2013). Furthermore, facilitative effects
131 are generally more intense in stressful environments, where high levels of stress or
132 disturbance limit plant growth in the absence of biotic habitat amelioration (Bertness &
133 Callaway, 1994; Brooker & Callaghan, 1998; He *et al.*, 2013). In addition, simultaneously
134 co-occurring stress gradients can result in complex changes in plant interaction intensity
135 (Mod *et al.*, 2014).

136 As with facilitative effects, BFEs may be context-dependent, but to our knowledge this
137 has hardly been explored. BFEs vary with changes in species richness of the beneficiary
138 community, indicating that the feedback effect is dependent on the number and identity of the
139 species that cause the BFE (Schöb *et al.*, 2014b). This may be due to diversity effects such as
140 niche partitioning, facilitation or sampling effects in which taxonomically and
141 phylogenetically more diverse beneficiary species assemblages have stronger effects (Flynn
142 *et al.*, 2011). Furthermore, it may depend on limiting niche similarity effects, in which
143 interactions of species sharing more similar niches with the benefactor are more competitive
144 (MacArthur & Levins, 1967; Adler *et al.*, 2012). These ideas have not been directly
145 addressed, even though the corresponding phylogenetic pattern, i.e. a higher phylogenetic
146 distance between beneficiaries and benefactors than expected by chance, has been described
147 (Castillo *et al.*, 2010; Valiente-Banuet & Verdú, 2013). Furthermore, we know that when two

interacting species compete for the same resource the effect of one species on the other is directly linked to the feedback effect of the latter species to the former (Keddy 2001). If there was a similar direct link between the facilitative effect and the feedback effect between a benefactor and a beneficiary, the intensity of the BFE would increase with increasing intensity of the facilitative effect. Surprisingly, and to our knowledge, only very recently has this facilitation-BFE link started to be explored (Schöb *et al.*, 2014a) and, despite a wealth of understanding of how competitive and facilitative interactions change with environmental conditions (Grime, 1977; Bertness & Callaway, 1994), we are not aware of any study assessing the response of BFE to environmental severity gradients.

The limited understanding of the context-dependence of BFEs calls for large-scale studies where we can relate properties of the beneficiary community and variability in environmental conditions to BFE. To this end, we reanalysed a global dataset on alpine cushion plants (Butterfield *et al.*, 2013; Cavieres *et al.*, 2014; Schöb *et al.*, 2014b). This dataset was used previously to assess the impact of cushion plants on phylogenetic and taxonomic diversity and community composition along global-scale environmental gradients (Butterfield *et al.*, 2013; Cavieres *et al.*, 2014), and to assess the fitness consequences of the benefactor cushions for acting as facilitators (Schöb *et al.*, 2014b). Whereas the former studies demonstrated the context-dependence of facilitative effects, the latter study showed that cushion plants experience reduced flowering and reproductive output with increasing abundance of beneficiaries, indicating a predominating negative BFE in cushions. Here, we combined aspects of all three studies by investigating the context-dependence of the BFEs. In other words, we determined sign and strength of BFEs on alpine cushion plants based on flower density of cushions and assessed the dependence of BFEs to beneficiary community composition, the strength of the facilitative effects of cushions, and local-scale biotic and climatic habitat conditions using structural equation modelling. We hypothesized that the strength and direction of BFEs will be related to the composition of the beneficiary community. We expected that those beneficiary communities consisting of species more closely related to their benefactor cushion species having stronger negative feedback effects than communities of species distantly related to their benefactor. We further hypothesized a relationship between facilitation intensity and BFE. On the one hand, we expected that stronger facilitation (e.g. larger plants) would directly increase negative BFEs. On the other hand, we expected that the intensity of facilitation would indirectly modulate the BFE if it affects the diversity and composition of the beneficiary community. Finally, we hypothesized

a relationship between the local-scale environmental conditions and BFE. We expected that more favourable local-scale environmental conditions would directly reduce facilitation and increase beneficiary community diversity, and therefore indirectly modulate the BFE.

Material and Methods

Manipulative approach

At each of six sites, including one site from Ecuador [Volcano Antisana, 4550 m, cushion species *Azorella aretioides* (Apiaceae)], two sites from Switzerland [Gemmi, 2300 m, *Carex firma* (Cyperaceae) and *Silene acaulis* (Caryophyllaceae)], one site from China [Qilian Shan, 4240 m, *Thylacospermum caespitosum* (Caryophyllaceae)], and two sites from Spain [Sierra Nevada, 2575 m and 3110 m, *Arenaria tetraquetra* ssp. *amabilis* (Caryophyllaceae)], we established 20 trios of plots between 2009 and 2010. Each trio consisted of one cushion with associated species, one cushion with associated species removed, and an open area plot away from cushions. Plot size was (mean ± SE) 672 ± 32 cm^2. All cushions and their associated open area plots were randomly selected among all medium-sized cushions within an area of *c.* 0.3 km^2. Half of the cushions were randomly assigned to the removal of associated species whereas the other half of the cushions served as a control. In proximity, but away from the control cushions, we sampled open areas of equal size to the control cushion. Within the canopy of the removal cushion, all aboveground biomass of other species was removed the year before and the year when flowers where counted, and clipping was repeated during the two growing seasons if regrowth was observed. For the control cushion and the paired open area, the number of individuals of all non-cushion species was recorded. In order to determine BFE for each trio of plots we counted flowers produced by the cushion plant in randomly placed quadrats within the canopy of removal and control cushions, calculated flower density, and estimated BFE as the difference in flower density between each control cushion and its paired removal cushion after standardizing flower density per site to zero mean and unit variance. Facilitation intensity expressed as the mean Relative Interaction Index (RII; Armas *et al.*, 2004) was calculated for each trio of plots as the relative difference in abundance of each non-cushion species between the cushion with associated species and the paired open area, averaged over all species present, where

(eq. 1) $$RII = (N_{cushion} - N_{open})/(N_{cushion} + N_{open}).$$

where $N_{cushion}$ is the number of individuals in the cushion and N_{open} is the number of individuals in the open area without cushions respectively. Positive mean RII values indicate prevailing facilitation whereas negative values indicate prevailing competition (Cavieres *et al.*, 2014). Finally, the cushion-associated beneficiary community of the control cushion was characterised by species richness, phylogenetic diversity and the mean abundance-weighted phylogenetic distance of the cushion-associated species assemblage to the cushion. For the phylogenetic analyses, we used the phylogenetic tree published by Butterfield *et al.* (2013). For phylogenetic diversity and phylogenetic distance to the cushion, we first pruned the tree for each control cushion using the drop.tip() function of the *ape* library (Paradis *et al.*, 2004) and then calculated phylogenetic diversity and mean phylogenetic distance to the cushion using the pd() function of the *picante* library (Kembel *et al.*, 2010) and the cophenetic() function in the *stats* package of R version 3.0.2 (R Core Team, 2013). Faith's phylogenetic diversity is the branch length (in Myr) spanned by the pruned phylogenetic tree including all non-cushion species within the corresponding cushion, whereas mean phylogenetic distance to the cushion is the phylogenetic distance between each non-cushion species growing in the cushion and the cushion (in Myr) averaged over all species growing in the cushion and weighed by their abundance.

Statistical analyses

To assess the sign and magnitude of the BFE for each site, we analyzed a linear model with standardized flower density as dependent variable and the removal treatment and site as fixed factors, followed by type-II analysis of variance. General contrasts of regression coefficients to test for treatment effects within each site were computed with the contrast() function of the *contrast* package (Kuhn, 2013). To assess the context dependence of BFE we performed path analysis (i.e. a structural equation model with only observed variables) using maximum likelihood estimation. We related BFE (i.e., the difference in the standardized flower density between the paired removal and control cushions) to Mean RII, and species richness, phylogenetic diversity, and mean phylogenetic distance to the cushion of the beneficiary community. The values of phylogenetic diversity and mean phylogenetic distance were divided by 100 in order to align the scales of variables. Path analysis was performed with the sem() function of the *lavaan* package (Rosseel, 2012).

Descriptive approach

For 33 sites distributed over Europe, North and South America and Asia, including temperate, Mediterranean and tropical climatic zones, we gathered data on the BFE,

taxonomic and phylogenetic community composition of the beneficiary communities, facilitation by cushion plants, the species pool and vegetation cover of the study sites, and local climatic conditions (Supporting Information Table S1) between 2003 and 2014. At all sites, haphazardly selected cushions within an area of *c.* 0.3 km^2 were paired with open area plots in close proximity, but away from cushions. Plot size was estimated by the two perpendicular dimensions of the cushion [$A = \pi(\text{diameter1} + \text{diameter2})/4)^2$] and varied with cushion size. Plot size of the open area plots equalled those of their paired cushions. Mean plot size was 1782 ± 83 cm^2. In all paired plots (81 ± 3 pairs per site) the number of individuals of each species was recorded [see Cavieres *et al.* (2014) for further information]. In a subset of cushion plots (46 ± 5 cushions), we further determined the flower density of cushions in randomly placed quadrats of variable size and number in the cushion canopy, and in some sites the relative cover of the beneficiary species assemblage growing within the cushion canopy was visually estimated [see Schöb *et al.* (2014b) for further information]. For each study site, the percentage cover of vegetation and open area was determined along 50 m transects.

Monthly climatic data for each site were obtained from the Worldclim database (http://www.worldclim.org; Hijmans *et al.*, 2005) with a spatial resolution of *c.* 1 km^2. For further analyses, we used precipitation during the summer months (June to August and January to March on the northern and southern hemispheres respectively) and maximum temperature at the onset of the growing season (June on the northern and January on the southern hemisphere, T_{max}Jun/Jan), because these two variables were shown to be the best predictors of precipitation and temperature for the vegetation structure in our study sites (Cavieres *et al.*, 2014). For the tropical sites of Venezuela, which do not show a thermal summer, the two variables reflect precipitation and temperature during the wet season.

The BFE was calculated as the relationship between cushion flower density and the abundance of cushion-associated beneficiary species (see below). For the beneficiary community we determined mean species richness, mean phylogenetic diversity and mean abundance-weighted phylogenetic distance to the cushion for each site (as explained above for the manipulative approach). Facilitation was quantified as the effect of cushions on the abundance and the presence of associated non-cushion species respectively. The former is quantified by the Mean RII index and the latter by the ISR index (Cavieres *et al.*, 2014). Mean RII was calculated as the relative difference in abundance of each species between cushion and open microhabitats according to equation 1, averaged over all species of a site.

With ISR we quantified the relative increase in species richness of a site due to the presence of cushions:

(eq. 2) $ISR = (S_{total} - S_{open})/S_{total}$,

where S_{total} is the community-level species richness and S_{open} is the species richness of the community without cushions. In order to overcome differences in the total area sampled across study sites, we estimated S_{total} and S_{open} using separate rarefactions based on the corresponding species × sample matrices (Badano *et al.*, 2006). In these sample-based rarefactions the number of species was estimated at the asymptote of the rarefaction curve using the Mau-Tao estimator in EstimateS v.8 (Colwell, 2006). We used S_{open} as an indicator of the species pool in the absence of cushion effects and relative vegetation cover of a site as an indicator of site-level productivity.

Statistical analysis

To assess the sign and magnitude of BFE for each site, we standardised (to zero mean and unit variance) cushion flower density for each site and related it to either the square-root transformed density and/or relative cover of cushion-associated species [including cushion size as a covariate in order to control for cushion size- and age-related changes in flower density (Samson & Werk, 1986; Morris & Doak, 1998)]. The regression coefficient of this relationship was then used as a measure of BFE for each site, where positive and negative values indicate positive and negative feedback effects of beneficiaries on the cushion, respectively.

Given the possibilities of direct and indirect effects of the different environmental variables that can affect BFEs, we applied structural equation modelling (SEM) to our dataset. SEM allows us to test complex *a priori* defined direct and indirect relationships in a unique framework and to assess the overall fit of the data to the model (Grace, 2006). Our *a priori* model relating climate and biotic site conditions, facilitation and the diversity of the beneficiary community to the BFE included the following premises (Supporting Information Fig. S2): (1) BFE is directly and indirectly related to the diversity of the beneficiary species assemblage: a) the number of beneficiary species and their phylogenetic spread can concomitantly influence diversity effects that may have consequences for the cushion; b) beneficiary communities consisting of species closely related to the cushion benefactor are likely to share more similar niches and are therefore more likely to directly interact with the cushion and induce a direct negative feedback effect; c) the species and phylogenetic

diversity of the beneficiary community indirectly affect BFEs through their direct relationship with the phylogenetic distance to the benefactor. (2) The facilitation effect of the cushion in terms of species abundance (Mean RII) and species presence (ISR) can directly and indirectly be linked to the BFE, where more intense facilitation may result in more intense BFE: (a) the relationship can be direct, for example if both interactions include the same, limiting resource; (b) the relationship can be indirect when the facilitative effects influence the species and phylogenetic diversity of the beneficiary community and their phylogenetic distance to the benefactor. (3) Biotic conditions on site can directly and indirectly influence BFE: (a) larger species pool and higher productivity (vegetation cover) can directly reduce the importance of the BFE; (b) they can indirectly affect the BFE through their influence on facilitation and the diversity of the beneficiary community. (4) Biotic conditions on site, facilitation, diversity of the beneficiary community and its similarity to the benefactor, and BFE may all directly or indirectly be affected by the local-scale climatic conditions, in particular temperature and precipitation.

As we had two distinct measures of BFE (either based on the relationship between beneficiary plant density or beneficiary plant cover and flower density of the benefactor respectively) and a range of sites with only one measure available, we tested the relationships among variables in a multi-group model with the two measures of BFE forming the two groups. In this multi-group model all regressions except those relating to BFE were constrained to be equal between the two groups, as we had had no reason to assume that any of these relationships should be different between the two groups. This is furthermore justified by model comparison of the constraint model with a completely unconstrained model ($AIC_{constraint} = 773$, $AIC_{unconstrained} = 785$, $\chi^2_{diff} = 37.2$, $d.f._{diff} = 25$, $P = 0.054$), indicating that the constraint model is more parsimonious. Summer precipitation and T_{max} Jun/Jan were combined in a composite variable representing the local climate, whereas all other variables were included as observed variables, mainly because the low *n* did not allow us to include more composites. The unit of measurement of the 'Climate' composite was based on the path coefficient of the better indicator variable (i.e. the variable with the higher standardized path coefficient) by fixing its path coefficient to 1. The relationships between the species pool and vegetation cover, between Mean RII and ISR, and between species richness and phylogenetic diversity of the beneficiary community were set as covariances. To overcome large scale differences among variables, very skewed distributions, and heteroscedasticity of variances we log-transformed species pool and vegetation cover values

and divided mean phylogenetic distance and summer precipitation values by 100 and the values of T_{max} Jun/Jan by 10 prior to inclusion into the SEM. Path coefficients were estimated using maximum likelihood, and the model fit was tested with a χ^2 goodness of fit test, a Bollen-Stine bootstrap test with 1000 bootstrap draws, a root mean square error of approximation (RMSEA) test, and the comparative fit index (CFI). A non-significant χ^2-, Bollen-Stine and RMSEA test, as well as CFI values above 0.90 indicate a good fit of the model to the data (Kline, 2011). The SEM was built, run and evaluated with *lavaan* (Rosseel, 2012) in R version 3.0.2 (R Core Team 2013).

Results

Manipulative approach

The effect of the removal of cushion-associated species on cushion flower density was dependent on site (significant interaction 'treatment × site'): $F = 4.27$, d.f. = 5, $P < 0.001$. The removal of cushion-associated species significantly increased flower density of the cushions at Qilian Shan, decreased flower density at Gemmi (*Carex*), and had no significant effect at the other sites (Fig. 1).

Path analysis revealed direct effects of beneficiary species richness and phylogenetic diversity (marginally significant) on the BFE (Fig. 2). In contrast, the mean phylogenetic distance of the beneficiary community to the cushion showed no direct effects on BFE. The negative effect of species richness on BFE was compensated in part by the positive effect of phylogenetic diversity on BFE. Nevertheless, the increasing diversity of the beneficiary species assemblage made BFEs more negative, they increased the negative feedback effects of the cushion-associated plant assemblage on the cushion. Facilitation intensity (Mean RII) had no direct effect on BFE, but seemed to positively affect BFE through its negative effects on species richness, even though this indirect effect was weak (standardized path coefficient = 0.15).

Descriptive approach

The relationship between the abundance of beneficiaries and flower density of cushions varied among sites and depended on whether the number of individuals or the relative cover of beneficiary species was used as a measure of abundance (Fig. 3). When using the number of beneficiary individuals for abundance, at 19 sites the regression coefficient was negative and at 12 sites the regression coefficient was positive. When relative cover of beneficiaries

was used for abundance, the coefficient was negative in 16 out of 21 sites. Thus, overall BFEs were negative, but highly site-specific.

Our data showed an overall good fit to our *a priori* SEM: $\chi^2 = 49.81$ (for # individuals $\chi^2 = 23.48$, for % cover $\chi^2 = 26.33$), d.f. = 39, $P(\chi^2) = 0.115$, P (Bollen-Stine Bootstrap) = 0.635; RMSEA = 0.103, $P = 0.183$; CFI = 0.966. BFE was concomitantly influenced by the species richness and phylogenetic diversity of the cushion-associated beneficiary community on the one hand and local environmental conditions on the other hand (Fig. 4). Depending on the method used to quantify BFE the local-scale environmental effects were stronger (# individuals, Fig. 4a) or of similar importance (% cover, Fig. 4b) than the factors measured for the beneficiary community (Table 1). Both estimates of BFE showed that increasing diversity of the beneficiary community and increasing intensity of the facilitative effects of the cushions directly reduced the BFE, i.e. they increased the negative feedback effects of the cushion-associated plant assemblage on the cushion. More favourable growth conditions, as indicated by a larger species pool, higher vegetation cover, more summer precipitation but lower maximum temperatures increased the overall BFE, i.e. they reduced the negative feedback effects of the cushion-associated plant assemblage on the cushion. These effects of the local biotic and climatic conditions were direct and indirect, with the direct effects being predominant and positive, and the indirect effects being rather weak, mostly negative, and mediated through the diversity of the beneficiary community and facilitation.

The effects of species richness and phylogenetic diversity tended to counterbalance each other. These counterbalancing effects were significant for the BFE measured using the number of beneficiary individuals as a measure of abundance (Fig. 4a) and marginally significant for BFE measured using the relative cover of beneficiaries (Fig. 4b). Taking into account the covariation between species richness and phylogenetic distance (unstandardized path coefficient = 1.20 ± 0.32, $P < 0.001$, standardized path coefficient = 0.93), species richness reduced BFE while phylogenetic diversity increased BFE, with the balance remaining negative for both methods applied to assess BFE. A similar effect was observed for facilitation, where ISR and Mean RII showed significant covariation (unstandardized path coefficient = 0.03 ± 0.01, $P < 0.001$, standardized path coefficient = 0.82), and where the positive effect of one variable was counterbalanced by the negative effect of the other. These counterbalancing effects between the two predictors of facilitation on BFE were significant only when BFE was estimated by the number of beneficiary individuals (Fig. 4a), but showed

405 a similar tendency when BFE was estimated by relative cover (Supporting Information Table
406 S2).

407 Discussion

408 Overall, the feedback effect of beneficiary species (BFE) on their cushion benefactor was
409 mostly negative, although these were highly context-dependent. This was shown by both the
410 manipulative and descriptive approaches as the BFE varied among sites and ranged from
411 significantly negative to significantly positive. In other words, the feedback effect on
412 benefactors ranged from a cost to a benefit, depending on the environmental context. Our
413 results provided support for our first hypothesis suggesting that the diversity of the
414 beneficiary community alters feedback effects (see also Michalet *et al.*, 2011; Schöb *et al.*,
415 2014b). However, our results also indicate that higher phylogenetic diversity *per se* makes
416 the BFE on cushion benefactors *less* negative, whereas higher species richness *per se* makes
417 BFEs *more* negative. In contrast to our expectations, the phylogenetic similarity of the
418 beneficiary community to the cushion did not affect the BFE of cushion benefactors in either
419 manipulative or descriptive approaches. As hypothesised, the intensity of the facilitative
420 effect of the benefactors was an additional driver of the BFE, even though in the manipulative
421 approach this link was only indirect and weak. The descriptive approach suggests that
422 stronger facilitation intensity corresponded with a more negative BFE, indicating the
423 presence of a direct link between facilitation intensity and the corresponding BFE.

424 All of these community-level patterns and processes of beneficiary diversity and
425 facilitation were modulated by the environmental conditions of sites, such as the available
426 species pool, site productivity and climatic conditions. Overall metrics of better growth
427 conditions at a site (i.e. larger species pool, higher site productivity and summer
428 precipitation) *indirectly* induced more negative BFEs but *direct* positive effects of these
429 conditions on BFE overrode the indirect negative effects. This resulted in overall less
430 negative or more positive feedback effects of beneficiaries on benefactors in generally less
431 stressful or more productive abiotic and biotic conditions. Consequently, similar to
432 competitive or facilitative effects (Michalet *et al.*, 2014), BFEs are dependent on a variety of
433 conditions ranging from the characteristics of the interacting beneficiary community to
434 environmental conditions at the site where the interaction takes place.

435 *The impact of beneficiary community composition on BFE*

The impact of the beneficiary community on benefactor cushions is most likely related to the sign and strength of the direct plant-plant interactions, such as resource-related competition, facilitation and niche complementarity effects. By controlling for covariation between species richness and phylogenetic diversity of the beneficiary community we demonstrated that some of the variance in BFE was uniquely explained by either species richness or phylogenetic diversity. Based on this, the interplay between the positive effect of phylogenetic diversity and the negative effect of species richness on BFE suggests that a species-rich community of closely related species imposed significant costs in terms of reduced flower production by the benefactor cushion. In contrast, more phylogenetically diverse but species-poor assemblages reduced this cost because of reverse facilitation effects of beneficiaries on the benefactor, or via increased niche complementarity. These diversity-effects of beneficiaries on benefactors might shift at other stages of reproduction (e.g. fruiting) though Schöb *et al.* (2014) showed that the significant reduction in flower production due to BFEs is unlikely to be compensated for by BFEs on later stages of reproduction, and therefore flower production serves as a good indicator of the final reproductive output of cushion plants.

The unique phylogenetic diversity component may indicate niche complementarity or sampling effects that may positively feed back to the benefactor. Such a relationship between phylogenetic diversity and niche complementary has been demonstrated in experimental grassland communities, where high phylogenetic diversity increased community-level productivity (Flynn *et al.*, 2011). They also showed that phylogenetic diversity was at least partially related to functional diversity, as proposed by the phylogenetic niche conservatism hypothesis (Ackerly, 2003). Therefore, a more phylogenetically diverse beneficiary community likely provides more trait variation and therefore increases the probability of harbouring species with facilitative effects (e.g. legumes). In contrast, a phylogenetically clumped but species rich beneficiary community likely has a reduced potential for these positive feedback effects because of a high probability of occurrence of species sharing similar traits and strategies for resource uptake. This could cause strong negative effects on the benefactor if this group of closely related beneficiary species shared much of the niche occupied by the benefactor cushion (MacArthur & Levins, 1967). However, the non-significant relationship between the phylogenetic distance of the beneficiary community to the benefactor cushion on the one hand, and the strength of the beneficiary feedback effect on the other hand, shows that this phylogenetic signal of limiting niche similarity was not evident in our studied ecosystem. The negative species richness effect may result, therefore,

from the overall negative impact (e.g. competition for resources) of a specific phylogenetic group of common beneficiary species that are not particularly close relatives of the cushion benefactor, e.g. grasses. However, further research is needed to explore the feedback effects of specific functional groups of beneficiary species.

The impact of facilitation on BFE

The indirect effects of facilitation on BFE through cushion effects on species richness and phylogenetic diversity were weak. This may seem surprising given a number of studies have shown increased diversity of species within cushions compared to open areas (e.g., Cavieres *et al.*, 2002; Michalet *et al.*, 2011; Schöb *et al.*, 2012). However, previously published studies from this global initiative on facilitation by alpine cushion plants detected positive effects of cushions on *site-level* phylogenetic diversity and species richness (Butterfield *et al.*, 2013; Cavieres *et al.*, 2014), where the higher plant diversity of sites with cushions was mainly due to different species inhabiting the cushion and open microhabitats respectively, rather than a higher diversity within the cushion microhabitat (Butterfield *et al.*, 2013). This could explain the lack of a significant relationship between facilitation and beneficiary community diversity within cushions in our global experimental design.

In contrast to the weak indirect effects of facilitation, we found quite strong direct effects of facilitation on BFE in the descriptive approach: stronger facilitation resulted in more negative BFEs. This suggests that there is indeed a direct link between the facilitative effect of the cushion benefactor and the feedback effect from the beneficiary. From studies in dry environments we know that one of the mechanisms of facilitation by cushions is increasing soil moisture and therefore improving water availability in cushions (Cavieres *et al.*, 2006; Schöb *et al.*, 2012, 2014a). Similarly, the negative feedback effect of beneficiary species on cushions was related to the competitive water uptake of species growing within cushions, thereby deteriorating the water status of the cushion (Schöb *et al.*, 2014a). Consequently, the link between facilitation and its feedback effect may occur if the two components of the bidirectional interaction function through the same resource, similar to competition (Keddy, 2001). However, many facilitative effects may not be mechanistically related to the BFE and this may in turn be responsible for the relatively weak direct effect of facilitation on BFE in our study. Many facilitative effects include shelter from herbivory or other attenuation of physical disturbances (e.g. stabilisation of substrate or protection from

strong winds) that are difficult to link to a similar mechanism of feedback effect from beneficiary species to the benefactor.

The impact of environmental conditions on BFE

Factors that function at the scale of regions such as climate, productivity, and species pool modulated both facilitation intensity and the diversity of the cushion-associated plant assemblage, and thus had indirect effects on BFEs. The species pool in open areas was strongly related to both facilitation intensity and beneficiary community diversity, where sites with larger species pools corresponded with weaker facilitation intensity by cushions and higher species richness and phylogenetic diversity of the beneficiary community. Similarly higher site-level productivity was also associated with higher beneficiary community diversity. These relationships correspond well with previous research showing reduced facilitation intensity in species rich alpine communities, such as in tropical mountains (Anthelme *et al.*, 2012), and reduced facilitation intensity together with species rich communities in sites with high productivity and large species pools (Cavieres *et al.*, 2014). These effects of local productivity and species pool on the species and phylogenetic diversity of the beneficiary community and facilitation increased negative BFEs and therefore the cost of facilitation.

The negative indirect effects of the local biotic and abiotic conditions on BFE were, however, overcompensated by their positive direct effects on BFE. In particular, more summer precipitation, higher productivity, and larger species pools corresponded with less negative or even positive BFEs. This suggests that the cushions of milder sites suffered a reduced cost simply due to the better growing conditions. This resembles some aspect of interactions of parasitic plants with their hosts, in which increasing ecosystem productivity correlates with reduced parasite impact on the host (Fibich *et al.*, 2010). We suggest that improved growth conditions via increased resource supply or decreased abiotic stress allows benefactors to better tolerate beneficiaries, i.e. the feedback effect becomes less important for the benefactor (*sensu* Kikvidze *et al.*, 2011).

Conclusion

A global dataset on alpine cushion plants has previously shown the important positive effects of cushion plants for alpine biodiversity (Butterfield *et al.*, 2013; Cavieres *et al.*, 2014). As a consequence of this facilitation effect, cushions were shown to suffer from reduced fitness for

being cooperative (Schöb *et al.*,2014b). Here we confirm that the community-level feedback effects of beneficiaries on benefactors were mostly negative, but were strongly context-dependent. The BFEs depended on the diversity and composition of the beneficiary community. Most clearly, more species-rich beneficiary communities increase negative feedback effects on cushion fitness. Apart from these community-level properties that directly affect the intensity of plant-plant interactions between beneficiaries and benefactors, local-scale environmental conditions also modulate these direct effects of beneficiaries. Under more benign environmental conditions, negative BFEs caused by the beneficiary community appear to be less important for the benefactor than under stressful conditions. Interestingly, this impact of the environmental conditions on the intensity of BFEs was of the same order of magnitude (if BFE is based on beneficiary cover) or even stronger (if BFE is based on the number of beneficiary individuals) as the direct impact of the beneficiary community composition on BFE (Table 1). This suggests a resource-driven nature of BFEs in which the intensity of competitive effects of the beneficiary community depends on their composition, and where these competitive effects are particularly important for the benefactor under resource-poor conditions. Our results therefore demonstrate strong context dependency of the feedback effects of beneficiary species on the nurse, similar to the two decades of work that have shown the effects of nurse plants on beneficiaries being highly context-dependent (Bertness & Callaway, 1994; He *et al.*, 2014). The sort of conditionality we demonstrate here for the generally negative beneficiary feedback effects, if played out over multiple years at a single site, suggests that the BFE is unlikely to be strong enough to have dramatically altered the evolutionary trajectory of the benefactors in this case, perhaps explaining why species with cushion growth forms continue to provide exceptional examples of convergent evolution despite attracting large numbers of other species to reside upon them and embedded in them.

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Supporting Information

Fig. S1 *Schematic representation of the bidirectional interaction between benefactor and beneficiary species.*

Fig. S2 A priori *structural model for the relationship of variables recorded with the descriptive approach.*

Table S1 *The study sites, climate data and cushion plant species*.

Table S2 *Standardized and unstandardized path coefficients of the structural equation model.*

Table S3 *Summary of significant direct, indirect and total effects on the beneficiary feedback effect.*

Fig. 1. Standardized flower density of cushions in response to the experimental removal of cushion-associated beneficiary species at six sites. Displayed are the mean ± 1SE. $n = 237$ (3 observations deleted due to missingness). *** = $P < 0.001$, * = $P < 0.05$, ns = $P > 0.05$.

Fig. 2. Path diagram of the relationships between the beneficiary feedback effect (BFE), species richness (SR), phylogenetic diversity (PD) and mean phylogenetic distance to the cushion (MPD) of the cushion-associated beneficiary community, and the facilitation effect of cushions (Mean RII). Solid and dashed black arrows show significantly positive and negative relationships respectively, dark grey arrows show marginally significant relationships, whereas light grey arrows show tested, but non-significant relationships. Line thickness of arrows is proportional to the standardized path coefficients. Standardized path coefficients are displayed (with the corresponding unstandardized coefficients in parentheses), together with the coefficient of determination for all endogenous variables. $n = 116$ (4 observations removed due to missing values).

Fig. 3. Regression coefficients of linear models relating standardized flower density of cushions to either the number of beneficiary individuals (a) or the relative cover of

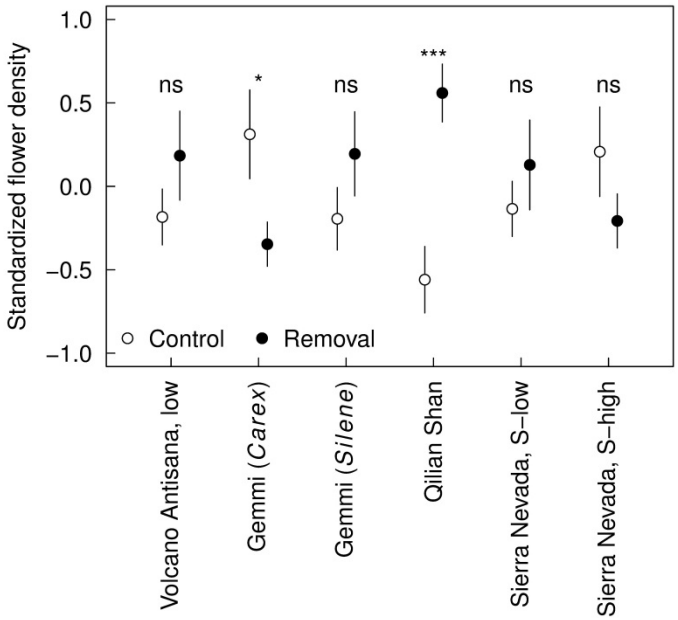
beneficiary species (b). Positive coefficients indicate higher reproductive output of cushions with increasing abundance of cushion-associated species (i.e. a positive BFE) whereas negative values indicate a negative BFE. Displayed are the mean, 50% and 90% confidence intervals.

Fig. 4. Structural equation model relating Climate (in black), biotic site conditions [in green; species pool in the open area (S_{open}) and vegetation cover], and facilitation (in orange; Mean RII and ISR), the beneficiary community diversity [in blue; species richness (Mean SR) and phylogenetic diversity (Mean PD)] and the mean phylogenetic distance (MPD) between the cushion-associated beneficiary community and the cushion (in olive) to the feedback effect of beneficiary species on the cushion (in red; BFE). The feedback effect was measured either as the relationship between the number of individuals (a) or relative cover (b) of the cushion-associated plant assemblage and cushion flower density. Solid and dashed black arrows show significantly positive and negative relationships respectively, whereas grey arrows show marginally significant relationships. Line thickness of arrows is proportional to the standardized path coefficients. Coefficients of determination for all endogenous variables are displayed. For standardized and unstandardized path coefficients and their significance for all relationships tested see Supporting Information Table S2. For BFE based on the number of beneficiary individuals $n = 31$, for BFE based on the relative cover of beneficiaries $n = 21$.

Table 1. Summary of significant direct, indirect and total effects of each group of predictor variables on the feedback effect of the number of individuals and relative cover of cushion-associated beneficiary species on cushion flower density (BFE). Displayed are standardised path coefficients and in parentheses their proportion relative to all other variables in %. The factor group 'Beneficiary community' consists of beneficiary species richness and phylogenetic diversity, the factor group 'Facilitation' consists of Mean RII and ISR, the factor group 'Biotic conditions' consists of species pool in the absence of cushions and vegetation cover, and the composite variable 'Climate' consists of precipitation during the summer months and T_{max} Jun/Jan respectively. For the summary table of direct and indirect effects for each predictor variable separately see Supporting Information Table S3

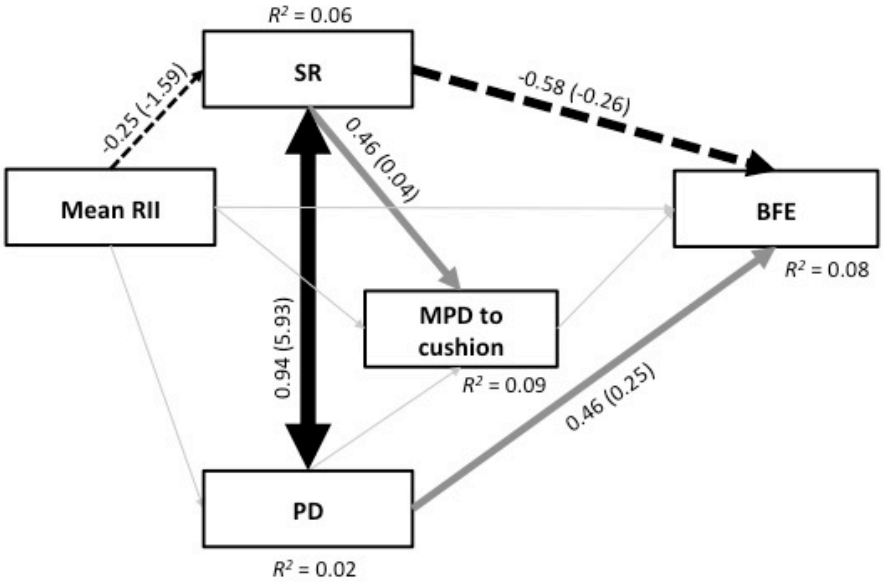
	# individuals						% cover					
Factor	Direct		Indirect		Total		Direct		Indirect		Total	
MPD to cushion	n.s.	(0)	n.a.	(0)	n.s	(0)	n.s.	(0)	n.a.	(0)	n.s.	(0)
Beneficiary community	-0.10	(9)	n.s.	(0)	-0.10	(11)	-0.43	(18)	n.s.	(0)	-0.43	(19)
Facilitation	-0.09	(9)	n.s.	(0)	-0.09	(10)	-0.70	(30)	n.s.	(0)	-0.70	(32)
Biotic conditions	0.46	(45)	-0.11	(80)	0.35	(39)	0.69	(29)	0.03	(15)	0.72	(32)
Climate	0.39	(37)	-0.03	(20)	0.36	(40)	0.53	(22)	-0.15	(85)	0.38	(17)

MPD = mean phylogenetic distance, n.s. = effect not significant, n.a. = effect not available.


Standardized flower density
1.0
0.5
0.0
−0.5
−1.0
ns
*
ns
***
ns
ns
Control
Removal
Volcano Antisana, low
Gemmi (Carex)
Gemmi (Silene)
Qilian Shan
Sierra Nevada, S–low
Sierra Nevada, S–high

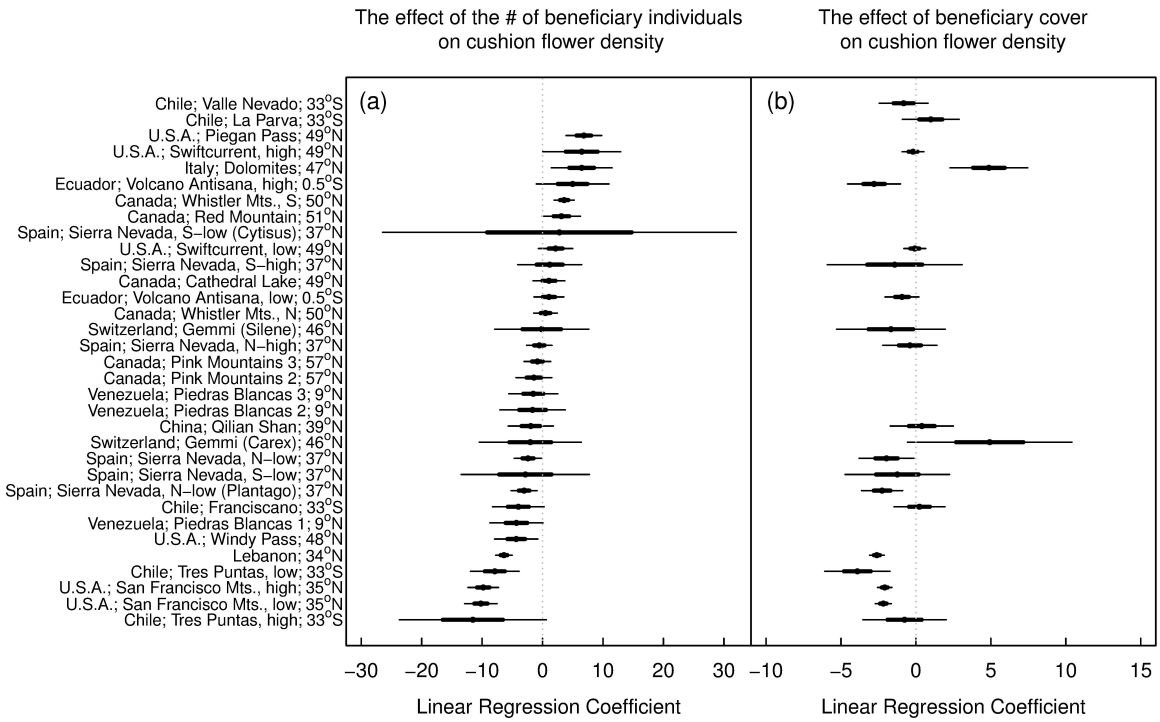
818

819 Fig. 1


R^2 = 0.06
SR
-0.25 (-1.59)
-0.58 (-0.26)
0.46 (0.04)
Mean RII
BFE
R^2 = 0.08
MPD to cushion
R^2 = 0.09
0.94 (5.93)
0.46 (0.25)
PD
R^2 = 0.02

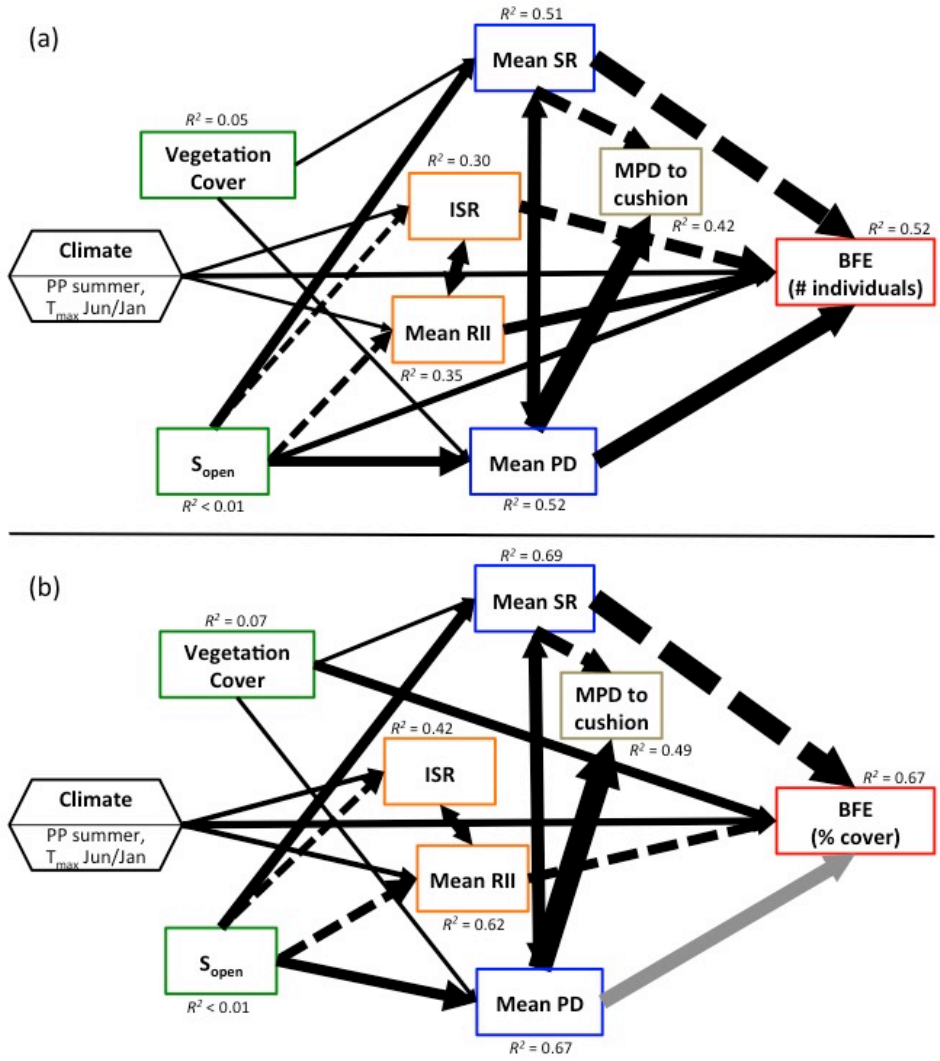
820

821 Fig. 2


The effect of the # of beneficiary individuals on cushion flower density
The effect of beneficiary cover on cushion flower density
(a)
(b)
Chile; Valle Nevado; 33°S
Chile; La Parva; 33°S
U.S.A.; Piegan Pass; 49°N
U.S.A.; Swiftcurrent, high; 49°N
Italy; Dolomites; 47°N
Ecuador; Volcano Antisana, high; 0.5°S
Canada; Whistler Mts., S; 50°N
Canada; Red Mountain; 51°N
Spain; Sierra Nevada, S–low (Cytisus); 37°N
U.S.A.; Swiftcurrent, low; 49°N
Spain; Sierra Nevada, S–high; 37°N
Canada; Cathedral Lake; 49°N
Ecuador; Volcano Antisana, low; 0.5°S
Canada; Whistler Mts., N; 50°N
Switzerland; Gemmi (Silene); 46°N
Spain; Sierra Nevada, N–high; 37°N
Canada; Pink Mountains 3; 57°N
Canada; Pink Mountains 2; 57°N
Venezuela; Piedras Blancas 3; 9°N
Venezuela; Piedras Blancas 2; 9°N
China; Qilian Shan; 39°N
Switzerland; Gemmi (Carex); 46°N
Spain; Sierra Nevada, N–low; 37°N
Spain; Sierra Nevada, S–low; 37°N
Spain; Sierra Nevada, N–low (Plantago); 37°N
Chile; Franciscano; 33°S
Venezuela; Piedras Blancas 1; 9°N
U.S.A.; Windy Pass; 48°N
Lebanon; 34°N
Chile; Tres Puntas, low; 33°S
U.S.A.; San Francisco Mts., high; 35°N
U.S.A.; San Francisco Mts., low; 35°N
Chile; Tres Puntas, high; 33°S
−30 −20 −10 0 10 20 30
−10 −5 0 5 10 15
Linear Regression Coefficient
Linear Regression Coefficient

822

823 Fig. 3


(a)
R^2 = 0.51
Mean SR
R^2 = 0.05
Vegetation Cover
R^2 = 0.30
ISR
MPD to cushion
R^2 = 0.42
R^2 = 0.52
BFE (# individuals)
Climate
PP summer, T_{max} Jun/Jan
Mean RII
R^2 = 0.35
S_{open}
R^2 < 0.01
Mean PD
R^2 = 0.52
(b)
R^2 = 0.69
Mean SR
R^2 = 0.07
Vegetation Cover
MPD to cushion
R^2 = 0.42
ISR
R^2 = 0.49
R^2 = 0.67
BFE (% cover)
Climate
PP summer, T_{max} Jun/Jan
Mean RII
R^2 = 0.62
S_{open}
R^2 < 0.01
Mean PD
R^2 = 0.67

824

825 Fig. 4